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THE EFFECT OF GROUP INTERACTIONS ON THE DEVELOPMENT OF SIZE DISTRIBUTION IN *MACROBRACHIUM ROSENBERGII* (DE MAN) JUVENILE POPULATIONS

ZIVA RA'ANAN AND DAN COHEN

*Department of Environmental Biology, Life Science Institute, The Hebrew University of Jerusalem, Jerusalem, Israel**

ABSTRACT

The distribution of body size among juvenile prawns, *Macrobrachium rosenbergii* (de Man), was assessed by comparing communally reared populations with singly raised individuals. Prawns reared in a group showed a relative excess of size variation, primarily associated with the appearance of two size classes which failed to appear among juveniles raised in isolation: 1) exceptionally fast-growing individuals, termed "jumpers," and 2) "laggards," which are generated in the presence of jumpers and represent a group of severely growth-repressed individuals. These results suggest that the variance of attained sizes of juveniles in a *M. rosenbergii* population is more affected by interactions within the prawn group than it is by genetic differences in growth potential of the individual prawns.

INTRODUCTION

Heterogeneous growth in aquatic species has been associated with factors that are intrinsic (Newkirk *et al.,* 1977), environmental (Wilbur and Collins, 1973), or social (Brown, 1946; Symons, 1972). In the present study we examine the growth of juveniles of the freshwater prawn *Macrobrachium rosenbergii* (de Man) and assess the extent to which an individual growth rate may be enhanced or suppressed by the presence of other individuals of the same species. Although growth suppression through competition has been documented (Wilbur and Collins, 1973; Wohlfarth, 1977), stimulation of growth which is observed under communal conditions but not in isolation is still a puzzling biological phenomenon.

We have chosen the freshwater prawn *M. rosenbergii* as the model organism for this study since, although the average weight of newly metamorphosed post larvae is 0.009 g with a small variance ($\sigma^2 = 6.0 \times 10^{-6}$ g, Sandifer and Smith, 1975; Malecha, 1977), the distribution changes gradually with time, as both variance and skewness increase. A "leading tail" in the distribution curve, containing individuals which are larger than the bulk of the population, is formed. Fast growing individuals, henceforth termed "jumpers," can grow as much as fifteen times larger than the population mode within a period of 60 days from metamorphosis (Willis and Berrigan, 1977; Ra'anan, 1982).

In a previous study on the same organism (Ra'anan, 1982; Ra'anan and Cohen, 1983) we showed that when populations of newly metamorphosed post larvae are reared at various stocking densities the average growth rate, the degree of size variation, and most important, the degree of skewness, all decreased with increasing density.

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* Present address: Aquaculture Production Technology (Israel) Ltd., P.O. Box 4330, Jerusalem 91042, Israel.

Our results contrasted with those obtained in similar studies on other aquatic organisms (Wilbur and Collins, 1973; Wohlfarth, 1977) where positive asymmetry of the weight distribution curves was more pronounced under the restricting growth conditions of high initial density, but diminished under improved conditions as initial stocking density decreased. Their results were interpreted as evidence for the effects of competition. On the other hand, our observations (Ra'anan and Cohen, 1983) led us to conclude that the appearance of jumpers in *M. rosenbergii* is not primarily a result of competition, if at all, but of factors intrinsically associated with population development. Sandifer and Smith (1975) suggested that this growth pattern may be caused primarily by genetic rather than environmental factors. However, Malecha (1977) reasoned that the size variance is due more to social interactions than to the segregation and independent assortment of genes controlling growth.

In order to differentiate between the relative contributions of genetic and social factors to the observed heterogeneous size distributions, we compared a communally reared post larval population with a parallel set of individually raised prawns. We used the change with time in the variance of the ln-transformed weights as a measure of intrinsic heterogeneity in the growth rates of the animals in the alternative growth regimes. If intrinsic factors are directly responsible for the variation in growth rates, we would expect a similar increase in the logarithmic variance in both the individual and the communal rearing systems. However, if interactions within groups are responsible for the observed growth heterogeneity, regardless of mechanism, the logarithmic variation of weights of individually reared juveniles should tend to remain constant with time while that of the communally grown animals should increase.

In this paper we establish the existence of growth enhancement in group-reared juveniles, and show that the observed rapid growth of the jumpers does not occur when prawns are raised individually. The wide size variance cannot therefore be attributed to genetic differences in the individuals' growth potential alone. We conclude that the growth stimulation is associated with the communal environment which is specifically responsible for the observed size heterogeneity and the appearance of jumpers in *M. rosenbergii* juvenile populations.

MATERIALS AND METHODS

Newly metamorphosed post larvae (PL) were obtained from the experimental hatchery at the Hebrew University of Jerusalem, operated by Aquaculture Production Technology (Israel) Ltd. PL from a single brood were divided into two experimental groups. One group was stocked individually in separate 4.5 liter aquaria (15 cm × 15 cm × 20 cm) with built in biofilters and no water connection between them ($n = 120$), while the other group ($n = 180$) was stocked into a tank of 720 liters (100 cm × 100 cm × 80 cm) with an external biofilter, for communal growth. The small aquaria were kept in the same room under equivalent controlled temperature (26 ± 1°C) and light regime (12L:12D) as the large communal tank. Both groups of prawns were fed daily with an excess of live *Daphnia* and ground fresh fish. Residual food and other particulate matter were removed weekly by siphoning. Additional submerged substrates, in the form of plastic boards, were placed inside the communal growth tank so that stocking densities per volume and per surface area were equivalent in both systems (1 PL per 4 liters and 1 PL per 0.08 m^2).

Since the total space available for each animal reared under communal growth conditions (720 liters) was much larger than that available for each individually reared PL (4 liters), a control experiment was designed in order to examine whether this factor alone could affect the growth rate of the isolated juveniles. In this experiment both communal and isolated prawns were monitored in identical aquaria (9 liters, 15 cm × 30 cm × 20 cm). Total available space was now identical for each of the animals, although their stocking density was greater under communal conditions (1 PL per 0.9 liters and 0.013 m^2) than it was for the isolated prawns (1 PL per 9 liters and 0.13 m^2).

The changes with time in the size distribution curves of both individually and communally grown populations in the two experiments were followed by weighing all animals individually once a week during 63 days. PL were weighed in water, using an automatic tare Sartorius balance. Data were analyzed on two levels. First we estimated the changes occurring in the variance and the skewness of the ln-transformed

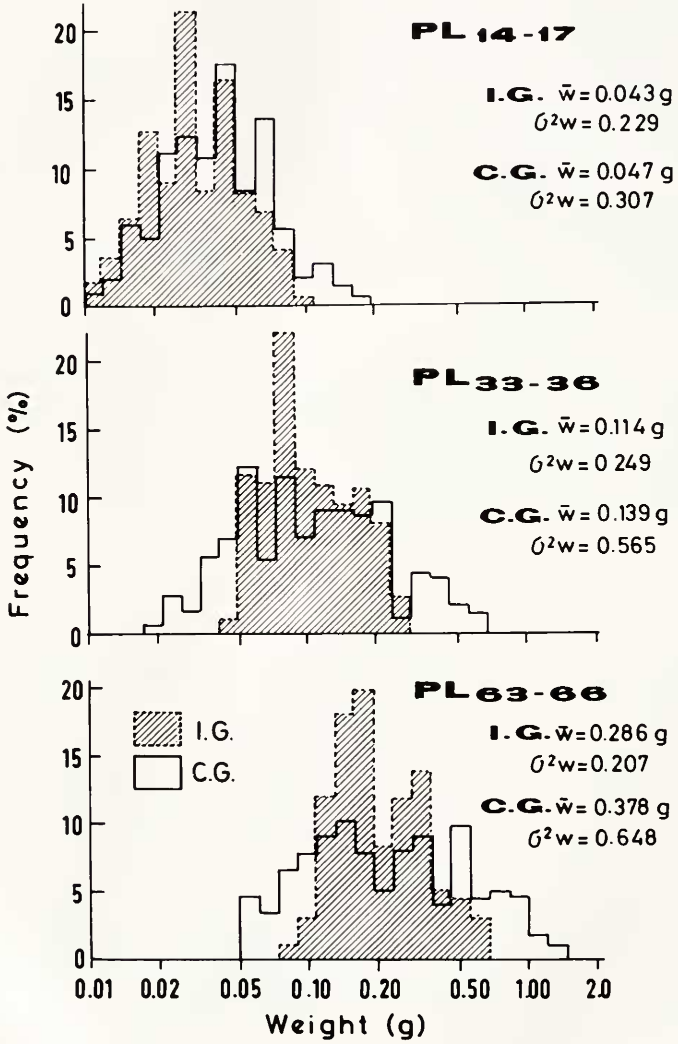


FIGURE 1. Frequency histograms of body weights of post larvae reared under individual (I.G., n = 120) and communal growth (C.G., n = 180) conditions. Upper, 14–17 days post metamorphosis; middle, 33–36 days; bottom, 63–66 days post metamorphosis.

weights in order to assess the degree of variation in growth within the respective populations. These parameters were calculated by the SPSS frequency routine for each weekly weighing. Next we calculated the individual relative growth rates, R, ($R = \frac{1}{T - t} \ln \frac{W_T}{W_t}$, where W_T and W_t are body weights at times T and t, $T > t$, according to Ricker, 1958; Wilbur and Collins, 1973) for all the juveniles in both populations. Comparative estimates of the R value distributions of communally and individually reared juveniles permit a direct evaluation of the respective growth heterogeneities.

RESULTS

The development of size variation

The frequency histograms of body weights for the individually reared post larvae (Fig. 1) and their statistical analyses (Table I) approximated a lognormal distribution. While the average weight increased with time, the logarithmic variance remained relatively constant throughout the experiment. Under communal growth conditions, however, both the average weight and the logarithmic variance continued to increase with time, and the initial lognormal distribution became positively skewed. The degree of skewness increased until the fifth week and then decreased slightly. The rate of increase of the average weight in both groups was similar until the sixth week (Fig. 2). Afterwards, the increase in average weight in the communally reared population exceeded that of the singles group. A comparison of the uppermost decile of the population by weight, the lowest decile, and the median value of the distribution in both populations (Table II) shows that the fastest growth is attained by the largest communally reared juveniles, to an average weight of 1.19 g, whereas the largest isolated individuals grew to an average of only 0.57 g during the 63 days. Growth of the smallest communally grown animals began to lag about four weeks after metamorphosis, while the distribution median value in both populations advanced at similar rates.

In the equal space per PL control experiment, size distributions for communal and individual PL were compared two and five weeks after metamorphosis (Fig. 3).

TABLE I

Changes with time in the mean ($\bar{X}$), standard deviation (S.D.), and skewness (Sk.) of weights in experimental juvenile prawns

	Individual growth (n = 120)			Communal growth (n = 180)		
Days after metamorphosis	$\bar{X}$ (g)	S.D. (σlnW)	Sk.	$\bar{X}$ (g)	S.D. (σlnW)	Sk.
14	0.043	0.478	−0.024	0.047	0.554	0.067
21	0.077	0.470	−0.032	0.077	0.647	0.107
28	0.096	0.464	0.079	0.094	0.682	0.178
35*	0.114	0.499	0.047	0.139	0.751	0.196
42*	0.202	0.482	0.120	0.241	0.770	0.242
49*	0.221	0.470	0.099	0.287	0.780	0.221
56*	0.250	0.471	0.045	0.327	0.788	0.184
63*	0.286	0.455	0.052	0.378	0.805	0.154

* Differences between means of individually and communally reared populations are statistically significant (*t*-test, $\alpha = 0.05$).

TABLE II

Increase in average weights (g) of the largest (upper 10%), smallest (lowest 10%), and the median body weight experimental subjects reared under individual (I.G.) versus *communal (C.G.) growth conditions*

	10% Largest		Median		10% Smallest	
Days after metamorphosis	I.G. (n = 10–12)	C.G. (n = 16–18)	I.G.	C.G.	I.G. (n = 10–12)	C.G. (n = 16–18)
14	0.08*	0.15	0.031	0.041	0.017	0.018
21	0.16*	0.25	0.066	0.063	0.031	0.027
28	0.20*	0.39	0.080	0.073	0.042	0.031
35	0.28*	0.47	0.109	0.103	0.061*	0.037
42	0.38*	0.72	0.152	0.160	0.083*	0.062
49	0.48*	0.87	0.177	0.191	0.097*	0.073
56	0.55*	0.99	0.208	0.223	0.114*	0.081
63	0.57*	1.19	0.227	0.252	0.138*	0.084

* Differences between means are statistically significant (t-test, $\alpha = 0.05$).

The percent coefficient of variation (P.C.V. $= 100 \times \frac{\text{S.D.}}{\text{W}}$) of communal PL reached 44.2, while that of the individual PL reached 22.0. Note that the difference in P.C.V. occurred during the first two weeks. Most of the enhancement of growth shown by the largest individuals in the communal group occurred in both experiments within the first two weeks and the corresponding lag in growth rate demonstrated by the smallest individuals communally reared became apparent only in later stages.

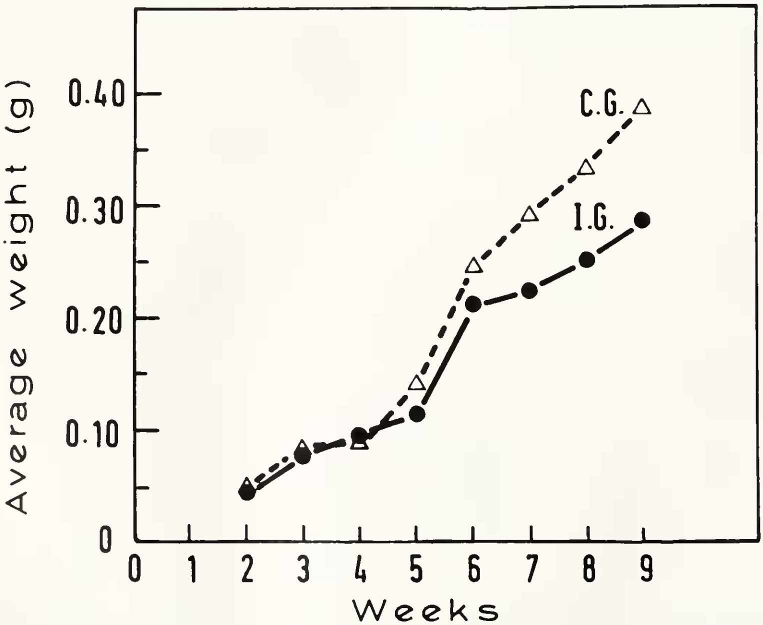
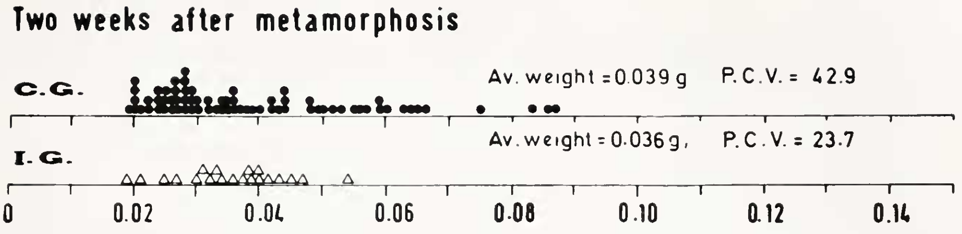


FIGURE 2. Rate of increase in average weight with time of individually (I.G.) and communally (C.G.) reared post larvae. Differences between means are statistically significant (t-test, $\alpha = 0.05$).



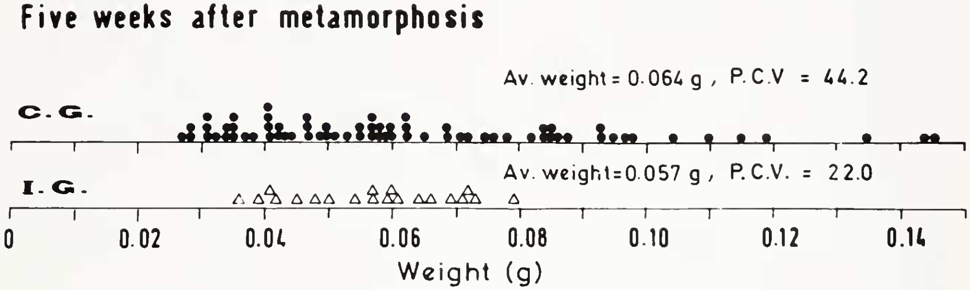


FIGURE 3. Weight distribution of juveniles reared communally (C.G., n = 70) and individually (I.G., n = 20), in the control experiment (equal space for both cultures), two and five weeks after metamorphosis. $\text{P.C.V.} = 100 \times \frac{\text{S.D.}}{\text{average weight}}$

Clearly, heterogeneity of growth in juvenile populations, as evaluated by the increased variance of the ln-transformed weight distributions with time, is much higher for communally reared juveniles than for those reared as individuals. Moreover, the largest individuals among the communal juveniles grew faster than the largest ones that were individually grown. This was also observed in the equal space control population, clearly indicating that the size of the container was not a limiting factor in the growth of the individually reared PL.

The distribution of relative growth rates

We calculated relative growth rates of individuals in both the isolated and the communal rearing systems in order to directly measure the variation of R values in the respective conditions, as well as to learn about the changes of R values with time in isolated *versus* communally grown prawns. In the communal culture we noticed that certain marked individuals maintained their relative size ranking, and on this basis we inferred that such stability is fairly general. Variance of 1.12 and 0.72 of communally and individually reared populations, respectively, two weeks after metamorphosis, decreased to 0.34 and 0.23, respectively, by the seventh week (Fig. 4). The R distribution of the communal population was wider, and was positively skewed at the initial growth period as compared with a narrower, more normal distribution attained by the individually reared juveniles. R values of the deciles by weight in the population, were plotted against the respective initial body weights of juvenile prawns reared communally between 14 to 21 and 56 to 63 days after metamorphosis (Fig.

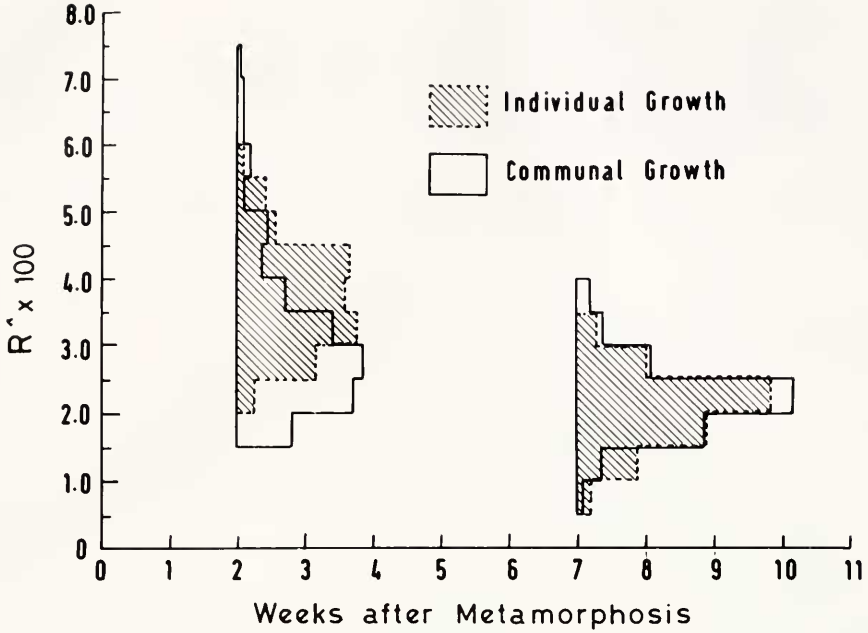


FIGURE 4. Frequency distributions of relative growth rates (R) in individually and communally reared juveniles, two and seven weeks after metamorphosis.

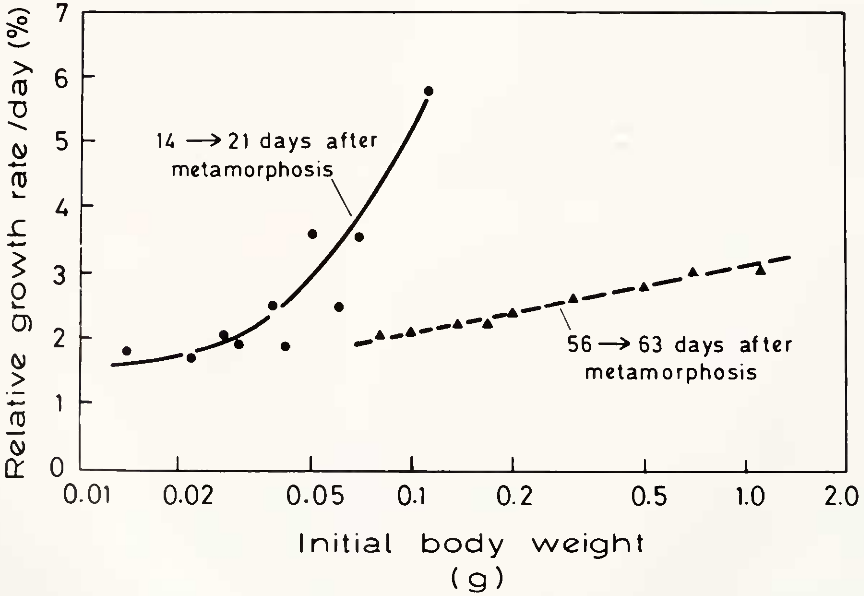


FIGURE 5. The relation between relative growth rates of body weight and initial body weight of communally reared juvenile prawns.

5). We find that R was positively correlated with the initial body weight in both periods, and that this correlation was more pronounced during the first time interval.

Discussion

The development of size variation

Growth in juvenile populations, as measured by the increase in variance of the ln-transformed weight distributions with time, is much higher for communally reared juveniles than for those reared as individuals. A similar phenomenon was observed by Malecha (pers. comm.) when larger juveniles, averaging 1.0 g, were selected for continual growth in separated cells.

Communally raised carps also had larger size variance than those reared individually (Nakamura and Kasahara, 1957; Yamagishi, 1962). The isolated carp, however, grew at rates similar to those exhibited by the fastest growing individuals under communal growth conditions. This result was explained by the absence of competition which had apparently inhibited growth of the smaller group-reared fish. In contrast, the excess in average weight of the communally reared *M. rosenbergii* juveniles relative to that of the individually grown animals (Fig. 2) indicates that jumpers' superior growth rates result from the presence of some stimulus which is lacking under conditions of individual isolation. This is supported by the observation that the decile containing the largest individuals in the communal group reached an average weight much higher than that achieved by the comparable decile of the isolated individuals during the same interval (Table II). Lee and Fielder (1983) reported an identical phenomenon in the prawn *Macrobrachium australiense,* ("Under laboratory conditions, group held juveniles produced more biomass than equivalent numbers of individually held prawns kept for the same time. However, the individually held prawns had a more uniform growth as shown by smaller standard errors in their mean sizes. . . . ") without referring to the growth stimulation which is the basis of the distribution pattern they observed. Allee (1951) illustrated many examples of the benefits of being in a group to the well being of the individual. He discussed cases of social facilitation leading to improved survival probabilities, improved chances of finding a mate, group stimulation of food consumption, and even improved learning capabilities. He also defined social behavior as any type of response which differs from that which would be shown if the animals were solitary. The greater the difference between their behavior when grouped than when isolated, the more social they are. Growth stimulation was also described by Uematsu (1971a, b) in the guppy, *Poecilia reticulata* (Peters), where the social facilitation of growth observed in the communal rearing system was associated with changes in feeding behavior and rates of respiration. In the himedaka (*Oryzias latipes*) social facilitation of growth was recognized and termed "the presence recognition effect" (Uematsu and Takamori, 1976).

Sastry and French (1977) and Aiken and Waddy (1977) found a strong correlation between the size of the container and the growth rate of the housed lobster, *Homarus americanus.* Van Olst and Calberg (1979) estimated that in order to avoid reduction in growth rate, the area of the container must be approximately the square of three times the body length of the lobster, or $(3BL)^2$. The maximum body length we observed in our experiment was 2.5 cm, which, in terms of the above formula, would dictate a surface area requirement of no more than 56 cm^2, whereas, in fact, the bottom area available to each animal was 300 cm^2. Nevertheless, in order to ascertain that the growth of the largest individuals in the separated aquaria was not inhibited by the size of the container or some other variable associated with it, the second experiment was conducted, in which both individuals and groups were raised in identical aquaria.

The results here were consistent with the main experiment. Communally reared jumpers grew significantly faster than the fastest individually housed juveniles, even though the space per animal available to the jumpers was much less than the space available to the singles. The possibility that container size adversely affected the growth of the largest individually reared prawns is therefore ruled out.

The influence of communal growth on individual size development in prawns is effective at both ends of the size distribution. The advent of jumpers is a consequence of growth facilitation and, thereafter, the lowest decile of the population specifically undergoes a growth lag (Fig. 1, Table II). The later appearance of the slow growth in small individuals is also correlated with the decrease in skewness of the size distribution curve starting from the fifth week (Table I). These observations suggest that such retarded growth might be due to a cumulative suppressive effect borne by small individuals in the presence of jumpers. We have shown elsewhere (Ra'anan, 1982) that after each of several periodic removal of jumpers from a communal growth system the remaining population immediately underwent a period of enhanced growth until a new group of jumpers developed.

In summary, the appearance of jumpers and the suppression of laggards as expressed in group culture, and their absence in isolation, support the notion that social factors (as defined by Allee, 1951) control size variation in *M. rosenbergii* juvenile populations more effectively than genetic factors governing potential individual size.

The distribution of relative growth rates

R ordinarily decreases with age and size (Brown, 1946; Yamagishi, 1962) and, indeed, the growth rates of the individuals in this experiment decreased with time as the animals' weights increased, under both culture conditions applied. The variance in R values at the initial growth period was more pronounced for the communally than for the individually reared populations, but with time it, too, decreased.

We also found a positive correlation between the R values and the positions of the individuals with respect to rank in size within the population, a phenomenon which may be fairly general. Brown (1946) had reported that individual relative growth rates in trout fry were usually higher for larger juveniles. Thus, the order of descending weight was also an order of decreasing relative growth rate for the group. This phenomenon was analyzed mathematically by Koyama and Kira (1956), who proposed four types of mathematically derived size frequency distributions, assuming exponential growth by individual plants in a population. They referred to the condition in which initial weight (W_0) and R have normal distributions, and in which R is positively correlated with size, as the N-N correspondent type. Just such a positive correlation was obtained between initial body weight and relative growth rates of our juveniles throughout the eight week period after metamorphosis (Fig. 5). The marked increase in the positive asymmetry of the juvenile weight distribution under communal growth conditions can be attributed to the enhanced growth rates of the larger juveniles, and especially the largest among them.

Since the correlated size ranking and relative growth rates in *M. rosenbergii* juveniles are subject to interactions within populations, the question arises as to what extent these parameters may be fixed or reversible traits in the ontogeny of individual juveniles. Experiments on this problem are in progress.

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